Interaction of Elevated Ultraviolet-B Radiation and CO_2 on Productivity and Photosynthetic Characteristics in Wheat, Rice, and Soybean[1]

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ABSTRACT

Wheat (*Triticum aestivum* L. cv Bannock), rice (*Oryza sativa* L. cv IR-36), and soybean (*Glycine max* [L.] Merr cv Essex) were grown in a factorial greenhouse experiment to determine if CO_2-induced increases in photosynthesis, biomass, and yield are modified by increases in ultraviolet (UV)-B radiation corresponding to stratospheric ozone depletion. The experimental conditions simulated were: (a) an increase in CO_2 concentration from 350 to 650 microliters per liter; (b) an increase in UV-B radiation corresponding to a 10% ozone depletion at the equator; and (c) a and b in combination. Seed yield and total biomass increased significantly with elevated CO_2 in all three species when compared to the control. However, with concurrent increases in UV-B and CO_2, no increase in either seed yield (wheat and rice) or total biomass (rice) was observed with respect to the control. In contrast, CO_2-induced increases in seed yield and total plant biomass were maintained or increased in soybean within the elevated CO_2, UV-B environment. Whole leaf gas exchange indicated a significant increase in photosynthesis, apparent quantum efficiency (AQE) and water-use-efficiency (WUE) with elevated CO_2 in all 3 species. Including elevated UV-B radiation with high CO_2 eliminated the effect of high CO_2 on photosynthesis and WUE in rice and the increase in AQE associated with high CO_2 in all species. Elevated CO_2 did not change the apparent carboxylation efficiency (ACE) in the three species although the combination of elevated CO_2 and UV-B reduced ACE in wheat and rice. The results of this experiment illustrate that increased UV-B radiation may modify CO_2-induced increases in biomass, seed yield and photosynthetic parameters and suggest that available data may not adequately characterize the potential effect of future, simultaneous changes in CO_2 concentration and UV-B radiation.

Current atmospheric levels of CO_2 may double from 340 μL L^{-1} to 680 μL L^{-1} by the middle of the 21st century (8). It is evident from a number of field and greenhouse experiments that increases in CO_2 will have a significant effect on layer with subsequent increases in the amount of solar ultra-growth and photosynthesis in a wide range of cultivated and native plant species which possess C_3 metabolism (10, 14, 24). Since rising CO_2 reduces the oxygenase component of RuBP[2] carboxylase/oxygenase, increases in photosynthesis and biomass can be expected up to atmospheric CO_2 concentrations of 1000 μL L^{-1} (15). This increase in photosynthesis may be maintained over a range of light conditions (24) and CO_2 concentrations (17). In addition to CO_2, other trace gases are also increasing as a result of industrialization. The rise of chlorofluorocarbons (CFCs), methane (CH$_4$), and nitrous oxide (N$_2$O) may substantially deplete the stratospheric ozone violet-B radiation (UV-B, between 290–320 nm) reaching the earth's surface (1, 3). Although this predicted increase is small relative to the entire electromagnetic spectrum, UV-B has a disproportionately large photobiological effect due to its absorption by proteins and nucleic acids. In UV-B sensitive plants, photosynthetic capacity may be reduced directly by the effect of UV-B radiation on photosynthetic enzymes or disruption of PSII reaction centers, or indirectly by effects on photosynthetic pigments and stomatal function (9, 13, 19, 20).

Both CO_2 and UV-B radiation are expected to increase simultaneously with future changes in global climate. To date, however, each factor has been determined separately with respect to plant growth and photosynthesis. Consequently, it is unclear whether increases in atmospheric CO_2 will result in increases in photosynthesis and growth if solar UV-B radiation increases concurrently. It is conceivable that each factor may not be directly additive; consequently, their combined effects may contrast sharply with predicted changes in net CO_2 assimilation and plant productivity based on a single factor assessment. It is of considerable interest, therefore, to quantify the photosynthetic and growth responses to simultaneous increases in CO_2 and UV-B radiation, especially among major food crops.

The purpose of this study was twofold: (a) to determine if increases in seed yield and biomass with elevated CO_2 are modified by increases in UV-B radiation, and (b) to determine if any photosynthetic increase resulting from long-term exposure at high CO_2 is modified by increased UV-B radiation over a range of light and CO_2 conditions.

[2] Abbreviations: RuBP, ribulose 1,5-bisphosphate; A, photosynthetic CO_2 assimilation rate; UV-B, ultraviolet B radiation (290–320 nm); C_a, external CO_2 concentration; C_i, intercellular CO_2 concentration; AQE, apparent quantum efficiency; PPF, photosynthetic photon fluence.

Table I. *Seed Yield and Total Biomass (g plant⁻¹) for Wheat, Rice, and Soybean Grown in Ambient and Elevated CO_2 with Ambient and Supplemental Levels of UV-B Radiation*

Percent change for each parameter is relative to ambient conditions.

Crop	Trt.	Seed Yield	Change	Total Biomass	Change
			%		%
Wheat	Control	11.6 c[a]		27.1 b	
	+UV-B	10.7 c	(−8)	27.4 b	(+1)
	+CO₂	17.5 a	(+51)	44.8 a	(+65)
	+CO₂, +UV-B	13.2 bc	(+14)	37.1 a	(+37)
Rice	Control	56.4 b		118.0 b	
	+UV-B	55.2 b	(−2)	114.3 b	(−3)
	+CO₂	66.6 a	(+18)	130.8 a	(+11)
	+CO₂, +UV-B	62.3 ab	(+10)	124.6 ab	(+6)
Soybean	Control	55.4 b		171.3 c	
	+UV-B	58.2 b	(+5)	163.1 d	(−5)
	+CO₂	71.2 a	(+29)	196.6 b	(+15)
	+CO₂, +UV-B	71.2 a	(+29)	215.2 a	(+26)

[a] Means with the same letter are not significantly different at the 95% level according to the Student-Newman-Keuls test.

MATERIALS AND METHODS

Seeds of rice (*Oryza sativa* L. cv IR-36), wheat (*Triticum aestivum* L. cv Bannock), and soybean (*Glycine max* [L.] Merr. cv Essex) were planted May 10, 1988, in 0.5 L pots in unshaded greenhouses at the Duke University Phytotron in Durham, NC. Pot size was increased periodically to a final volume of 20 L to prevent potential feedback limitations to photosynthesis resulting from restricted root growth (16). Plants were grown in a potting medium of pea gravel and sand (2:1, v:v). All plants were placed on carts and rotated daily. The carts were rotated weekly and every third week the treatments were rotated to reduce the effects of greenhouse heterogeneity on plant growth. Soybean and wheat were

watered twice daily and fertilized once daily with half-strength Hoagland solution. A plastic bag was placed inside pots growing rice to allow flooding of the pots several days after seed germination. This water was drained and refilled each week to reduce nutrient and algal accumulation. Rice plants were fertilized twice a week.

Three hundred and twenty plants of each species were subjected to the following treatments throughout the growing season: (a) ambient CO₂, ambient UV-B (control); (b) ambient CO₂, elevated UV-B (+UV-B); (c) elevated CO₂, ambient UV-B (+CO₂); (d) elevated CO₂, elevated UV-B (+CO₂, +UV-B). Five replicates of 16 plants each were randomly distributed within a treatment. Growing conditions in each of the two phytotron greenhouses were 27°C day/23°C night temperature, 60% RH, and a total daily photosynthetic photon fluence (PPF, between 400–700 nm) approximately 80 to 85% of ambient.

Carbon dioxide concentrations of 350 (ambient) and 650 (elevated) µL L⁻¹ were maintained throughout the experiment by using a CO₂ injection system. Supplemental UV-B radiation was provided by Q-panel UVB-313 sunlamps suspended above and perpendicular to the plants and filtered with pre-solarized 0.08 mm thick cellulose diacetate (transmission down to 290 nm) following the procedure outlined in Lydon *et al.* (11). The spectral irradiance at plant height under the lamps was measured with an Optronic Laboratories Inc. Model 742 Spectroradiometer interfaced with a Hewlett Packard model 85 printing calculator. The spectroradiometer was equipped with a dual holographic grating and modified to maintain constant temperature by the addition of Peltier heat exchange units. The spectroradiometer was calibrated against a National Institute of Standards and Technology traceable 1000 W tungsten filament quartz halogen lamp and wavelength alignment checked at 253.7, 296.7, 302.2, and 334.1 nm using mercury vapor emission lines from a mercury arc lamp. The absolute spectral irradiance was weighted with the generalized plant response action spectrum (3) and normal-

Table II. *Light Saturated Photosynthetic Rate, AQE, ACE, and WUE for Wheat, Rice, and Soybean Grown in Ambient CO_2 and Elevated CO_2 with Ambient and Supplemental Levels of UV-B Radiation*

Percent change for each parameter is relative to ambient conditions. AQE and ACE are defined in "Materials and Methods." WUE is defined as the ratio of CO_2 gained per amount of H_2O lost (μmol μmol⁻¹)* 100. All measurements ($n = 10$–20) were averaged for the 5 week period and at flowering.

Crop	Trt.	Photo-synthesis	Change	AQE	Change	ACE	Change	WUE	Change
		μmol m⁻² s⁻¹	%	μmol CO₂ μmol PPF⁻¹	%	μmol CO₂ μL Cᵢ⁻¹	%		%
Wheat	Control	23.4 b[a]		0.056 b		0.185 a		0.563 b	
	+UV-B	23.3 b	(+0)	0.048 b	(−14)	0.179 a	(−3)	0.550 b	(−2)
	+CO₂	37.4 a	(+60)	0.071 a	(+27)	0.178 a	(−4)	0.867 a	(+54)
	+CO₂, +UV-B	36.1 a	(+54)	0.059 b	(+5)	0.138 b	(−25)	0.769 a	(+36)
Rice	Control	27.2 b		0.053 b		0.144 a		0.426 b	
	+UV-B	26.3 b	(−3)	0.056 b	(+6)	0.139 a	(−3)	0.429 b	(+1)
	+CO₂	32.7 a	(+20)	0.068 a	(+28)	0.120 ab	(−16)	0.571 a	(+34)
	+CO₂, +UV-B	29.8 ab	(+9)	0.057 b	(+8)	0.107 b	(−35)	0.500 ab	(+17)
Soybean	Control	29.6 b		0.033 b		0.170 a		0.523 b	
	+UV-B	29.6 b	(+0)	0.031 b	(−6)	0.161 a	(−5)	0.502 b	(+4)
	+CO₂	41.7 a	(+41)	0.047 a	(+42)	0.165 a	(−3)	0.870 a	(+67)
	+CO₂, +UV-B	39.6 a	(+34)	0.038 ab	(+15)	0.163 a	(−4)	0.850 a	(+63)

[a] Means with the same letter are not significantly different at the 95% level according to the Student-Newman-Keuls test.
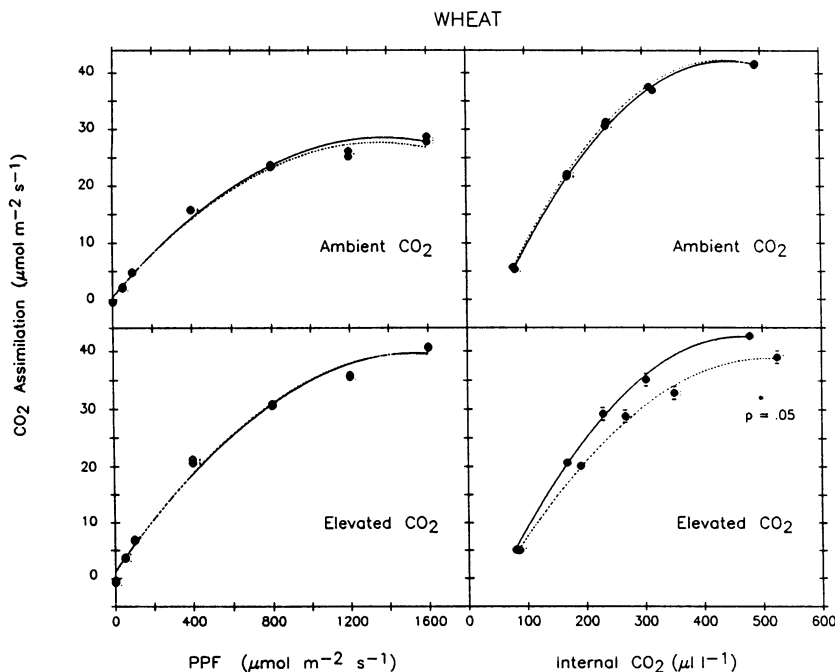
Figure 1. Response of wheat grown and tested at ambient (350 μL L^{-1}) or elevated (650 μL L^{-1}) CO_2 to increased PPF and internal CO_2 concentration with ambient (solid line) and supplemental levels of UV-B radiation (dashed line). Data represent averages taken at 5 weeks and at flowering since no significant differences were observed between these 2 times (n = 10–12). Error bars = ±1 SE. An asterisk (*) indicates significant difference for any two points (P ≤ 0.05).

ized to 300 nm to obtain the daily biologically effective fluence (UV-B_{BE}).

Because of the UV absorption characteristics of the greenhouse glass, plants received no natural UV-B radiation, so all UV-B radiation was artificially supplied by the lamps. UV-B lamps provided a UV-B fluence which approximated the UV-B radiation that is received at Durham, NC (35°N) under present ozone conditions (control) and that anticipated at Singapore (0°N) with a 10% ozone depletion under clear sky conditions during the seasonal maxima (8.8 and 15.7 effective kJ m^{-2} UV-B_{BE}, respectively, according to an empirical model of Green *et al.* [7]). The different irradiances were obtained by adjusting the heights of lamps above the top of plants to maintain fixed distances of 0.50 and 0.35 m, respectively.

All plant species were harvested at seed maturity and plant material was dried at 70°C for at least 48 h prior to weighing.

Gas exchange measurements were made after 5 weeks of irradiation and at flowering (about 10 weeks after irradiation) on five replicate plants from each treatment. Statistical analysis revealed no significant differences between measurements made at 5 weeks and at flowering, consequently the data from these two measurement periods were combined for analysis. Net CO_2 assimilation (A) and transpiration (E) were measured at leaf temperatures of 28 ± 0.3°C. Temperature was measured with a fine wire copper-constantan thermocouple and maintained by Peltier heat exchange units within the cuvette. A small fan maintained air flow and mixing in the cuvette. Because of UV absorption by the cuvette cover, gas exchange measurements represent a cumulative, rather than an instantaneous effect of UV-B radiation. The flux of CO_2 was measured in an open system using an ADC Series 225 infrared gas analyzer. Transpiration and stomatal conductance to water vapor (g_s) were calculated from the flux of H_2O vapor into and out of the cuvette as determined from General Eastern System 100DP dew point hygrometers. All gas exchange

parameters were determined according to the calculations of von Caemmerer and Farquhar (22).

The response of CO_2 assimilation to light was determined by initially measuring at the actual growth CO_2 concentration (Ca = 350 or 650 μL L^{-1}) and a PPF of 2000 μmol m^{-2} s^{-1}. The PPF was then decreased sequentially by neutral density filters to 1600, 1200, 800, 400, 100, 50, and 0 μmol m^{-2} s^{-1} as measured with a Li-Cor model 185 quantum sensor. Following initial trials, the subsequent maximum irradiances used were those required to saturate photosynthesis (1200, 1600, and 1600 μmol m^{-2} s^{-1} for rice, wheat, and soybean, respectively). The apparent quantum efficiency (AQE) was determined at constant temperature over the 50 to 100 μmol m^{-2} s^{-1} PPF range in each species according to Sullivan and Teramura (18).

The response of CO_2 assimilation (A) to internal CO_2 (Ci) was determined initially at saturated PPF and the growth Ca. The external CO_2 concentration was then reduced to 100 μL L^{-1} and A was measured at CO_2 concentrations of 100, 250, 350, 450, and 700 μL L^{-1}. The apparent carboxylation efficiency (ACE) was determined as the initial slope of the A/Ci response between a Ca of 100 and 250 μL L^{-1}. The stomatal limitation to photosynthesis was calculated as the percent decrease between A when Ci = Ca (350 or 650 μL L^{-1}) and A at the Ci recorded at the growth CO_2 concentration (6).

The concentration of methanol-extractable UV-B absorbing compounds (primarily flavonoids) were determined on samples of leaf material 5 weeks after emergence and at flowering for each species. UV-B absorbing compounds were determined according to the procedure of Mirecki and Teramura (12) using acidified methanol (79:20:1 v:v:v, methanol:water:HCl). Absorbance was measured with a Pye Unicam Model PU 8600 scanning spectrophotometer. The absorbance at 300 nm was arbitrarily used for comparative analysis of the methanol extract (18).
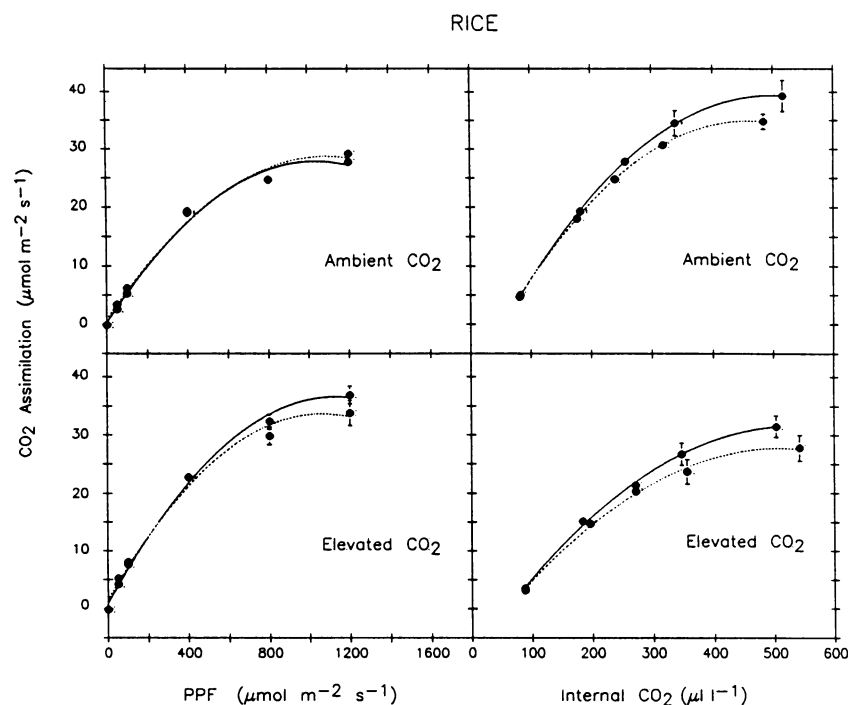
RICE

Figure 2. Same as Figure 1, but for rice.

All data were analyzed by a two-way analysis of variance which tested main effects of UV-B radiation and CO_2 and their interaction. Significantly different means were separated using the Student Newman-Keuls multiple range test at $P \le$ 0.05.

RESULTS

Seed yield and total plant biomass increased significantly with elevated CO_2 in all three crop species (Table I). Increased UV-B at ambient CO_2 reduced total plant biomass in soybean but had no effect on rice or wheat. However, increased CO_2 and UV-B in combination eliminated CO_2-induced increases in seed yield in wheat and seed yield and total biomass in rice so that these values were not significantly different than the controls (Table I). In contrast, under an elevated CO_2/UV-B environment, total plant biomass increased in wheat and total plant biomass and seed yield increased in soybean relative to the control (Table I).

Photosynthesis was significantly increased by CO_2 enrichment in all species compared to the controls at ambient levels of UV-B and in wheat and soybean under an elevated CO_2/ UV-B environment (Table II). UV-B did not reduce photosynthesis at either CO_2 concentration in these crops. In rice, however, photosynthesis was reduced by increased UV-B at high CO_2 (compared to +CO_2 alone) so that no statistical difference was observed relative to the control (Table II).

The photosynthetic response over a range of PPF and Ci values was generally not altered by UV-B or CO_2 (Figs. 1, 2, and 3), except at saturating PPF and Ci where A was reduced at a Ci of 450 to 500 μL L^{-1} in wheat (Fig. 1), and the PPF response at high CO_2 above 1200 μmol m^{-2} s^{-1} in soybean (Fig. 3). A comparison of the A to Ci response in ambient and elevated CO_2 grown plants suggests no acclimation (5)

to increased CO_2 in wheat and soybean and only slight acclimation in rice (Fig. 2).

In all three species, the AQE was increased by elevated CO_2 but UV-B in combination with elevated CO_2 reduced AQE so that no difference was observed with respect to the controls (Table II). No significant differences in AQE for any species were observed with elevated UV-B at ambient levels of CO_2. Elevated CO_2 had no significant effect on apparent carboxylation efficiency (ACE) in any of the three species. Also, under ambient CO_2 conditions, increased UV-B irradiation had no effect on ACE, but at elevated CO_2, increased UV-B reduced ACE in wheat and rice compared to the controls (Table II). Water-use-efficiency (WUE) was unaffected by UV-B but increased significantly with elevated CO_2 in all three species. At elevated levels of CO_2 and UV-B, WUE was still significantly greater than the control in wheat and soybean, but no increase in WUE was noted in rice (Table II).

UV-B increased the concentration of UV absorbing compounds in wheat and rice but had no effect in soybean (Table III). Elevated CO_2 also increased UV absorbing compounds in wheat, but in rice the CO_2-induced increase was only significant when increased UV-B was combined with elevated CO_2. Although increased CO_2 and/or UV-B did not statistically increase UV absorbing compounds in soybean, the concentration of these compounds in control plants was approximately fourfold greater than that of wheat and rice (Table III).

DISCUSSION

Increases in biomass and seed yield reported in this experiment are similar to previously published values for wheat, rice, and soybean grown in an elevated CO_2 environment (4, 10). However, the effects of increased UV-B radiation in either CO_2 environment were dependent upon the plant species.
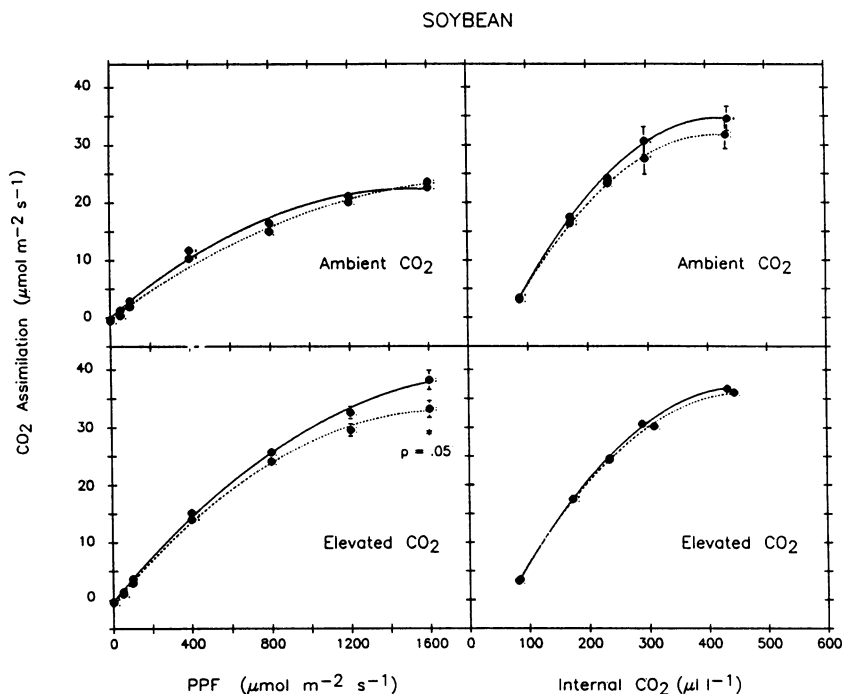
TERAMURA *ET AL.*

SOYBEAN

Figure 3. Same as Figure 1, but for soybean.

Increased UV-B radiation tended to reduce the CO_2-induced increase in biomass and seed yield in wheat and rice, but soybean seed yield and biomass still increased under the combination of elevated CO_2 and UV-B radiation.

The increase in photosynthetic capacity with high CO_2 was also modified by UV-B radiation depending upon the plant species studied. The insensitivity of photosynthesis to increased UV-B at ambient CO_2 has been reported previously in wheat (2), but the effects of UV-B on photosynthesis in rice have not been evaluated. UV-B radiation may alter the

Table III. *Absorbance at 300 nm for Ambient CO_2 and UV-B Radiation with Supplemental a: UV-B radiation; b: CO_2; and c: a and b in combination*

Because of changes in leaf thickness associated with growth in high CO_2, absorbance rates are expressed on a per weight basis (A_{300} g^{-1}). Percent change is given relative to the control. Absorbance measurements (n = 10–12) were averaged for the 5 week period and at flowering.

Crop	Trt.	A_{300} g^{-1}	Change
			%
Wheat	Control	18.5 b[a]	
	+UV-B	27.2 a	(+42)
	+CO_2	29.3 a	(+53)
	+CO_2, +UV-B	25.8 a	(+37)
Rice	Control	15.1 b	
	+UV-B	21.1 a	(+40)
	+CO_2	17.5 ab	(+20)
	+CO_2, +UV-B	20.7 a	(+40)
Soybean	Control	68.3 a	
	+UV-B	65.9 a	(−3)
	+CO_2	70.5 a	(+4)
	+CO_2, + UV-B	78.2 a	(+15)

[a] Means with the same letter are not significantly different at the 95% level according to the Student-Newman-Keuls test.

photosynthetic apparatus in rice so that it is no longer capable of responding to increases in CO_2 and, consequently, the overall CO_2 effect on growth and seed yield is reduced accordingly. Reductions in photosynthesis in soybean (cv Essex) have been reported with increased UV-B (18), but no effects were observed in this study.

An evaluation of the specific effects on photosynthesis may be useful in interpreting the overall effects on biomass and seed yield. For example, the analysis of the initial slope of A to light or Ci can be used to interpret changes in photosynthetic capacity (6, 22). In this experiment, calculation of diffusional limitations to photosynthesis based on the response of A to C_i (6) did not indicate any changes with increased UV-B radiation at either CO_2 concentration (data not shown). This suggests that any limitation to photosynthesis was not due to stomatal limitations but was probably related to the biochemistry of CO_2 fixation.

UV-B radiation may irreversibly damage PSII reaction centers (13, 21, 23) and such damage could be observed in reduced AQE or substrate regeneration limitations since the energy produced by the light reaction products (*e.g.* NADPH, ATP) is required to regenerate substrate. In this experiment, increased UV-B irradiance only reduced AQE in wheat and rice when compared to the elevated CO_2 environment.

Production of flavonoid compounds which absorb UV-B radiation may provide some degree of photoprotection in certain plant species and may partially account for the variability in plant response to UV-B radiation (1, 20). Of the three species studied, only soybean failed to show a significant increase in flavonoid compounds under increased UV-B radiation at ambient CO_2 and it was the only species in which biomass was reduced by UV-B. In contrast, at ambient CO_2, increased UV-B radiation increased UV-B absorbing compounds by 42 and 40% in wheat and rice, respectively, and no reductions in growth or seed yield were observed. However, the absolute concentrations of UV-absorbing compounds

were much greater in soybean leaves than in rice or wheat, and soybean was able to maintain significant CO_2-induced increases in seed yield at an elevated CO_2, UV-B environment while rice and wheat did not. Possible differences in localization of UV absorbing compounds combined with overall anatomical and morphological differences between the two cereal grains and soybean could contribute to the specific UV-B protection afforded by these compounds.

In this experiment, variability of the photosynthetic and yield responses with increased CO_2 and UV-B is not surprising given the range of sensitivities reported for increases in UV-B radiation (1, 20) and CO_2 (10, 15, 24) when determined individually. For example, approximately half of the 300 species and cultivars tested for sensitivity to UV-B radiation show a decrease in production and/or photosynthesis (20), while 9 to 120% increases in economic yield have been projected with a doubling of present CO_2 levels (10). These response differences may also be modified by changes in microclimate (15, 18). It is reasonable, therefore, to anticipate that sensitivity to concurrent increases in CO_2 and UV-B radiation may also be dependent upon species and cultivar, and modified by microclimate. This variability in sensitivity suggests that crops and their weedy competitors might also respond differentially to concurrent changes in CO_2 and UV-B radiation.

Since UV-B may modify CO_2-induced increases in photosynthesis and yield, not accounting for the effects of UV-B radiation could potentially result in over-estimates of photosynthesis and plant productivity based on the response to increased CO_2 alone. This study demonstrates the complexity of the interaction of CO_2 and UV-B on photosynthesis and productivity, and points out the need for additional information on how combinations of factors anticipated with future changes in the global environment may affect physiological processes in plants.

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